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THE ZOOLOGICAL RELATIONSHIPS
OF THE CONODONTS

A PART OF A DISSERTATION SUBMITTED
TO THE FACULTY OF THE DIVISION OF THE
PHYSICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY

1935

By
HAROLD W. SCOTT

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THE ZOOLOGICAL RELATIONSHIPS OF THE CONODONTS¹

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ABSTRACT

The ideas of previous workers on the zoological relationships of conodonts are presented. Eighteen "conodont assemblages" from the Quadrant shales of Montana are described and figured. The "assemblages" are compared to the tooth structure of various types of vertebrates but are found to be dissimilar in every respect. They are more like, in fact are almost identical to, the jaw apparatus of annelid worm jaws.

Few subjects in paleontology have lent themselves to more controversy than the zoological affinity of conodonts. Probably no group of fossils has been as much studied and as little understood. Since the time of their discovery by C. H. Pander (1)² in 1856, they have formed the basis for many discussions. Paradoxically as it may seem, they have seldom been claimed to be the remains of vertebrate animals by students of the vertebrates, or the remains of invertebrates by invertebrate paleontologists. Instead, there has always been a tendency for each group of workers to study them but force ownership upon the other group.

Conodonts have been considered to be the remains of such diverse groups as Pisces, Annelida, Mollusca, Arachnida and Crustacea. Since the publication of Ulrich and Bassler's (2) classification in 1926, however, they

have been generally considered as the remains of fish.

Early in October, 1933, samples of a black fissile shale of the Quadrant formation, commonly considered Pennsylvanian in age, from the Big Snowy Mountains in central Montana, were studied for microfossils. This shale contains many individual conodonts but, what is far more important, it has yielded seventy-five complete or partial conodont jaw assemblages. This last group of specimens forms the basis of this paper.

In addition to the jaw assemblages and individual conodonts found, there are numerous pelecopods and a few linguloid brachiopods.

All but one of the different generic types of conodonts found have been identified. They include *Prioniodus*, *Prioniodella*, *Hindeodella*, and *Polygnathus*. It is not proposed at this time, however, to describe any new species or genera of conodonts. On the other hand, a discussion of the "conodont assemblages" from the Quadrant shales should go a long

¹ This paper was made possible through funds furnished by the Montana Bureau of Mines and Geology.

² Numbers in parentheses refer to the Bibliography at the end of the paper.

way in answering the old question, "What are conodonts?"

The writer is pleased to acknowledge his indebtedness to Eugene S. Perry, Chief Geologist of the Montana Bureau of Mines and Geology, through whose kindness the samples of Quadrant shale were obtained for study. He is also indebted to Carey Croneis of the University of Chicago for constructive criticism and for his kindness in reading the preliminary conclusions at the 1933 meeting of the Paleontological Society in Chicago. His best thanks are also due A. S. Romer of Harvard University for making important suggestions. The drawings were outlined by the writer and painted by Mrs. Elizabeth Lochrie of Butte, Montana.

HISTORICAL RESUMÉ

Pander considered conodonts as the remains of fish of the selachian or shark type. He entertained no doubt as to their zoological affinities as indicated by the title of the article, "*Monographie der fossilen Fische des silurischen Systems des russischbaltischen Government*," under which he named and described them.

J. Harley (3) appears to be one of the first to question Pander's disposal of conodonts. In 1861 he expressed the belief that they were the spines from animals similar to *Limulus* and *Squilla*.

In 1875 Pander's disposition of conodonts was questioned by J. S. Newberry (4), of Ohio. After studying many specimens from the Cleveland shales, he suggested that they might be annelids instead of fish (*Cyclostomata*).

G. J. Hinde (5), in 1879, considered them as teeth of primitive vertebrates and compared them with the teeth of the existing myxinoids. He made extensive researches on the annelid jaws

from the Isle of Gotland, England, Canada, and northeastern United States, and found many types of conodonts associated with them. He compared the chemical composition of these two different types of fossil remains and found that they were radically different. Furthermore, he found no gastropods in association with conodonts in the same formation. Nor did he find any Crustacea which might have possessed spines resembling conodonts. For these reasons he concluded that the fossils were not of invertebrate origin but belonged to the vertebrates. Nevertheless, he entertained some doubt as to their origin. This doubt is expressed in the statement, "the facts at hand appear insufficient to decide the question."

In 1884, U. P. James (6) regarded them as "the jaws and lingual teeth of mollusks." Few others have followed that suggestion.

In 1886 Rohon and Zittel (7) concluded that "the conodonts have structurally nothing in common either with the dentine of *Selachia* and other fishes, the horny teeth of *Cyclostomi*, the lingual teeth of the *Mollusca*, the hooklets of the *Cephalopoda*, or the broken segment spines of the *Crustacea*; on the other hand, both in form and in structure, they agree remarkably with the masticatory apparatus of the *Annelida* and *Gephyrea*."

In 1921 the question of the zoological affinities of conodonts was again seriously questioned. At that time W. L. Bryant (8) remarked: "On the whole, the longer I have studied these organisms, the more have I become convinced that the true conodonts have hardly anything really diagnostic in common with annelid jaws." This conclusion was arrived at by a comparison of the structure of conodonts and annelid jaws (scolecodonts). He considered conodonts to be the remains of "some primitive type of fishes."

As early as 1878, Ulrich (9) said that a "striking resemblance" existed between conodonts and the chitinous jaws of liv-

ing annelids. Though he was dissatisfied with this superficial resemblance, he concluded, at that time, that the "most probable explanation," was that conodonts "are the hooklets of species of annelids." But after many years of study, Ulrich and Bassler (2), in 1926, discussed the biological position of conodonts and published the first complete and satisfactory classification. They made a careful study of the teeth and dermal plates of recent fishes (Myxines) and concluded that conodonts were to be considered as "the teeth of primitive fishes and not necessarily all of the same group."

Many scientific workers have considered the affinity of conodonts as undeterminable and have hesitated to suggest their possible relationships. This is exemplified by the remark of A. S. Woodward (10), who says that "their histological structure is so different from that of any teeth known that their affinities are quite undeterminable." This question of doubt is not entertained by some of the most recent workers. Mr. Bryant (8) has "become convinced that the true conodonts have hardly anything really diagnostic in common with annelid jaws . . . the conclusion seems almost unavoidable that the conodonts must be considered as the dentition of some primitive type of fish."

In 1923, J. M. MacFarlane (11) classifies them as an order "Conodontes" under the Malacodermata. He accepts them "as the circumoral teeth of primitive members of that more primitive group of fishes, the Cyclostomata."

C. R. Stauffer and Helen Jeanne Plummer (12), in 1932, remark, "It is

evident that the solution of the problem lies near the fish."

In 1933, A. S. Romer³ said, "I cannot accept them as the remains of vertebrates."

It has been stated by many writers that the difference in the chemical composition of scolecodonts and conodonts is sufficient basis to warrant separation of the two groups; consequently, it is said, that they belong to animals of a different phylum. Stauffer and Plummer (12) remark that "one of the strong arguments in favor of including the conodonts with the fish is their chemical composition." This point is considered by the writer as of sufficient significance to aid in placing various forms in different orders or families within a phylum, but would be of no greater value in classification.

The foregoing is a sufficient, though not a complete, historical resumé of the ideas of various workers concerning the zoological affinities of conodonts. It indicates that just about as much doubt exists today over this important subject as has existed throughout the period since their discovery.

DESCRIPTION OF "CONODONT ASSEMBLAGES"

Assemblage One

Plate 58, figure 1

In this group there are six conodonts in a fair state of preservation. There is one well-preserved *Hindeodella* and the upper edge of a second can be seen on

³ Personal communication.

EXPLANATION OF PLATE 58

FIG. 1—Five specimens of *Hindeodella* and a *Prioniodus* (?).

2—Eight *Hindeodellas*.

3—(a) Four *Hindeodellas*, (b) *Prioniodus*, (c) *Prioniodella* (?).

4—Four right-hand *Hindeodellas*. Compare with figure 2.

5—(a, a') *Hindeodella*, (b, b') *Prioniodella*, (c) unidentified, (d) undescribed.

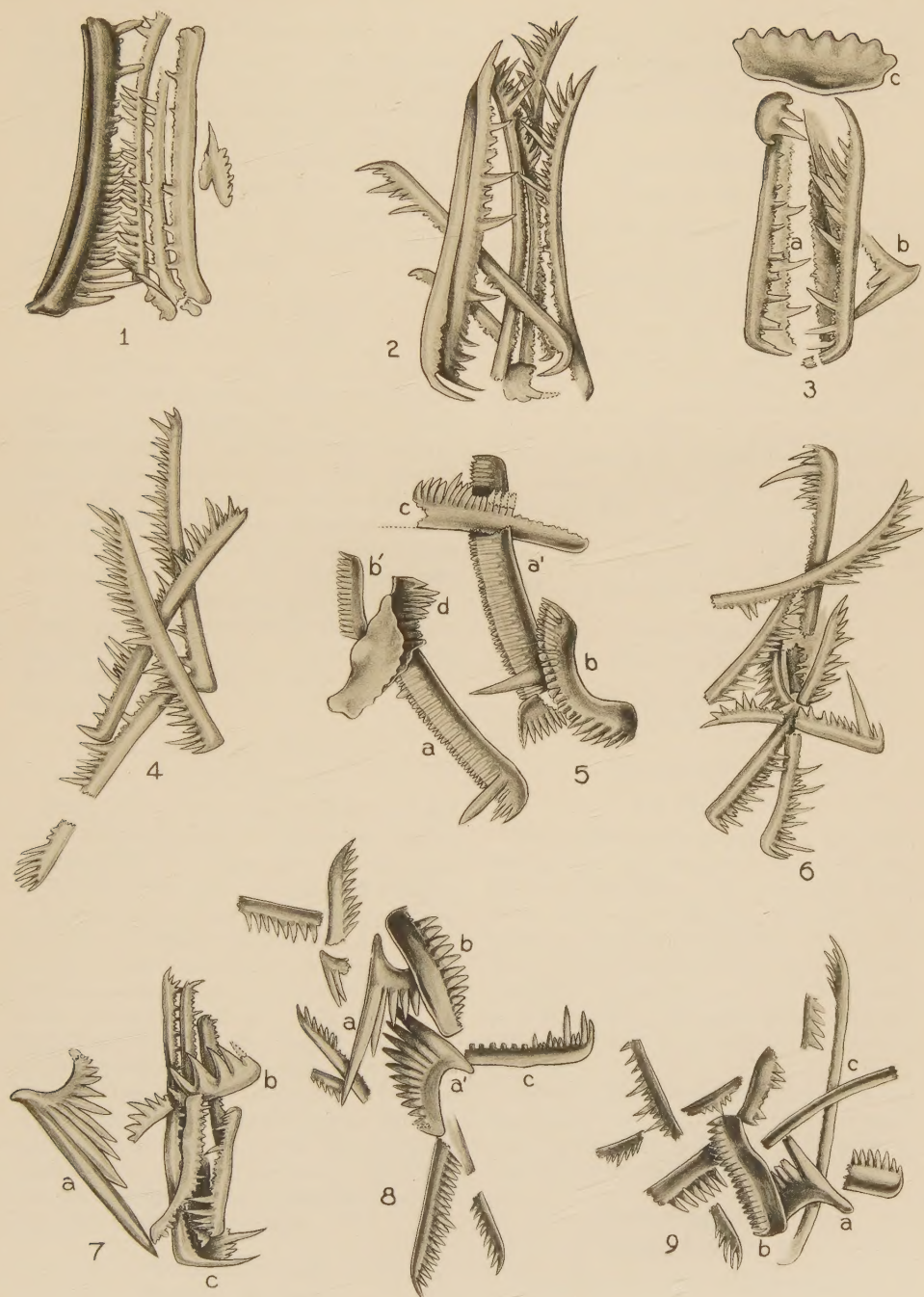
6—Six specimens of *Hindeodella*.

7—(a) *Prioniodus*, (b) *Prioniodella*, (c) three complete and two fragments of *Hindeodella*.

8—(a, a') *Prioniodus*, (b) *Prioniodella*, (c) *Hindeodella*.

9—(a) *Prioniodus*, (b) undescribed, (c) *Hindeodella*.

All figures about $\times 27$.





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the left side of the assemblage. On the right-hand side are three *Hindeodellas*, the bars of which are successively lower and the teeth of the uppermost specimen overlapping the teeth of the lower one. The main cusp is not distinct in any of the specimens. A fragmentary specimen of what appears to be a species of *Prioniodus* occurs on the outside of the assemblage to the right.

Assemblage Two

Plate 58, figure 2

Assemblage Number Two consists of eight well-preserved specimens of *Hindeodella*. The denticles of four of these specimens point to the left and the denticles of the remaining four point to the right. All of the individuals are well preserved, easily identified and seem to have maintained their natural position. They probably represent the actual position of the teeth in the mouth of the animal. There is a slight tendency for the bars to converge anteriorly. They may have been set in a semicircle as in the mouth of an annelid.

Assemblage Three

Plate 58, figure 3

This unusual group consists of two pairs of *Hindeodella*, a *Prioniodus*, and a *Prioniodella* (?). There are two *Hindeodellas* on each side of the assemblage. The denticles all point inwardly and are slightly inclined anteriorly. At right angles to the elongation of the assemblage is a specimen of *Prioniodella* (?). The identification of *Prioniodella* is doubtful for due to the fragile character of the entire assemblage it cannot be uncovered more than is shown. To the lower right of the assemblage is the imprint of a *Prioniodus* with its denticles pointing to the left posterior. An unidentified fragment is located in the left anterior of the assemblage.

Assemblage Four

Plate 58, figure 4

In this assemblage are four *Hindeodel-*

las with their teeth pointing to the left. This is interpreted as representing half of a group similar to the one picture in Assemblage Number Two.

Assemblage Five

Plate 58, figure 5

Most of the specimens in this assemblage are well preserved. The two *Hindeodellas* differ from all others described in this paper. The bar is deeply set with numerous small denticles and a large main cusp which is preceded by six sharply pointed denticles. Two *Prioniodellas* are also present; one each on the right and left side of the assemblage. A specimen of an undescribed conodont (d) covers the anterior end of *Hindeodella* (a). This is a form similar to that mentioned in Assemblage Number Seventeen. An unidentified specimen (c) is anteriorly located.

Assemblage Six

Plate 58, figure 6

There are six specimens of variously oriented *Hindeodellas* in this group.

Assemblage Seven

Plate 58, figure 7

This assemblage consists of six conodonts. The left specimen is a well-preserved *Prioniodus*. The denticles point to the right posterior and the main cusp is on the outside. On the right-hand side of the assemblage are three more or less complete specimens and two fragments of *Hindeodella*. The teeth point outward and are inclined anteriorly on all but one specimen.

Lying in the center and normal to the elongation of the *Hindeodella* group, with its denticles pointing anteriorly, is a specimen of *Prioniodella* (?).

Assemblage Eight

Plate 58, figure 8

Two specimens of *Prioniodus*, one of *Prioniodella* and parts of at least four specimens of *Hindeodella* are present.

Assemblage Nine

Plate 58, figure 9

One specimen of *Prioniodus*, two of *Prioniodella*, and fragments of at least three *Hindeodellas* are present in this group.

Assemblage Ten

Plate 59, figure 10

Only three individuals are found in this assemblage, a *Bryantodus*, a *Hindeodella*, and an undescribed form similar to the ones mentioned in Assemblages Number Seventeen and Number Five.

Assemblage Eleven

Plate 59, figure 11

Assemblage Eleven is a fairly complete and well-preserved group. It consists of the following paired forms: *Prioniodus*, *Hindeodella* and *Prioniodella* (?). The left member of *Prioniodus* is on the outside of the assemblage with the denticles pointing posteriorly and the main cusp on the inside. The denticles of the right member of *Prioniodus* (preserved as an imprint and illustrated as seen) point outward with the main cusp toward the anterior end. The specimens of *Hindeodella* lie with their denticles pointing outward and the two converge to a point posteriorly. In the anterior end of the right side of the assemblage are imprints of two broken specimens of what appears to be *Prioniodella*. There is also an imprint of an unidentified specimen in the center of the assemblage with the denticles pointing anteriorly. It is impossible to determine with any degree of accuracy the genus of this latter individual.

Assemblage Twelve

Plate 59, figure 12

A *Prioniodus*, two *Hindeodellas* and two broken specimens of unidentified conodonts make up this assemblage.

Assemblage Thirteen

Plate 59, figure 13

The same association of genera is found in this group, but the specific characteristics of each member are different than any of the other described groups. The main cusp on *Hindeodella* is preceded by seven small denticles. The specimens of *Bryantodus* and *Prioniodus* also differ from specimens in the other assemblages.

Assemblage Fourteen

Plate 59, figure 14.

Two complete specimens of *Hindeodella* and one of *Prioniodus* compose this group. The relationship of the *Hindeodella* specimens as seen in this assemblage is very common. The teeth of the upper specimen generally rest on the bar of the lower. The main cusps are so closely associated that the lower is commonly completely obscured by the upper.

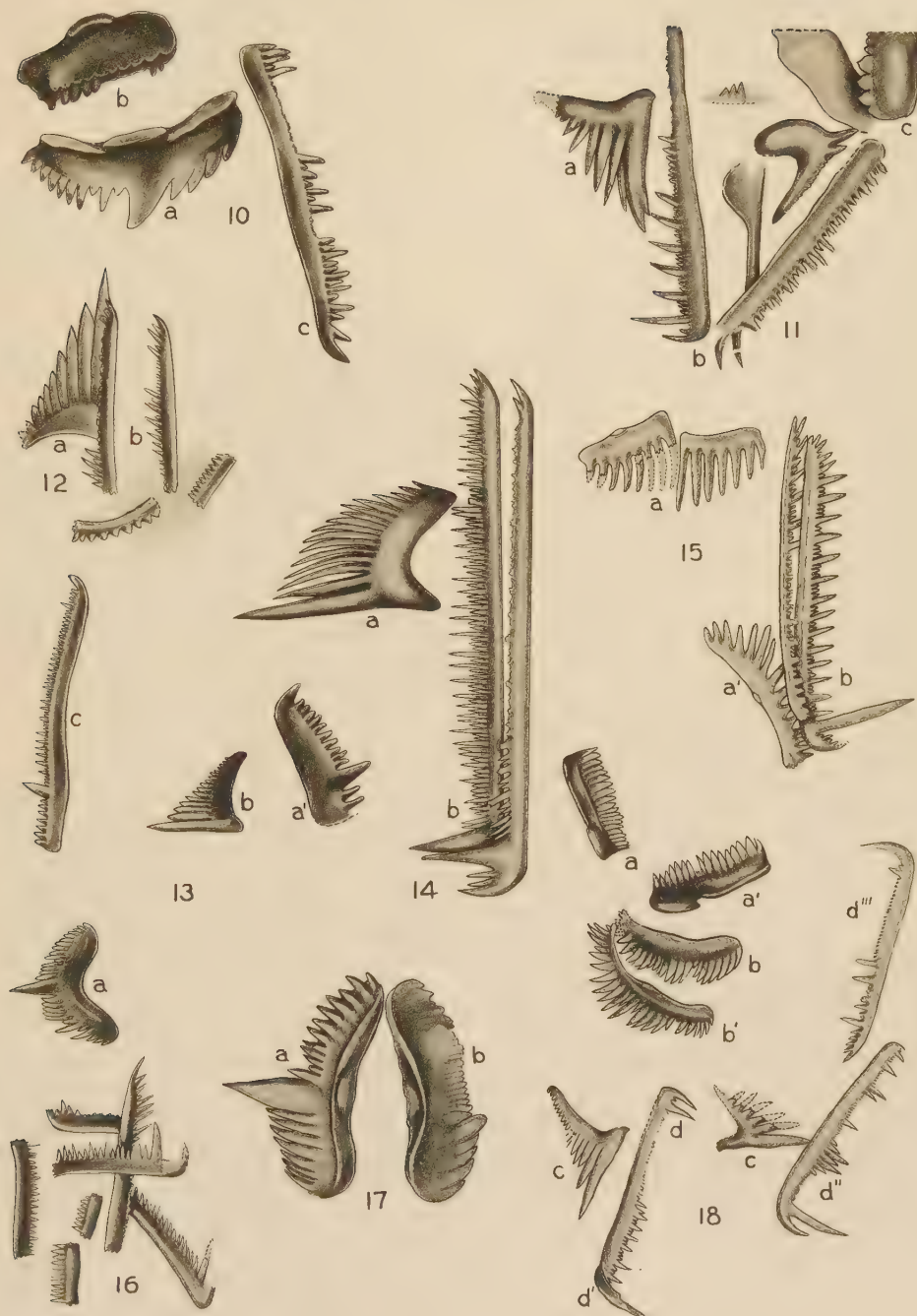
Assemblage Fifteen

Plate 59, figure 15

This assemblage is composed of two *Hindeodellas*, a *Bryantodus*, and a *Prioniodella* (?). The *Hindeodella* relationship is similar to that in Assemblage Number Thirteen, but the spacing of the denticles differs. Assemblages Thirteen and Four-

EXPLANATION OF PLATE 59

- FIG. 10—(a) *Bryantodus*, (b) undescribed, (c) *Hindeodella*.
 11—(a) *Prioniodus*, (b) *Hindeodella*, (c) *Prioniodella* (?).
 12—(a) *Prioniodus*, (b) *Hindeodella*.
 13—(a, a') *Bryantodus*, (b) *Prioniodus*, (c) *Hindeodella*.
 14—(a) *Prioniodus*, (b) *Hindeodella*.
 15—(a, a') *Bryantodus*, (b) *Hindeodella*.
 16—Fragments of three or more *Hindeodellas*.
 17—(a) *Bryantodus*, (b) undescribed.
 18—(a, a') Undescribed, (b, b') *Bryantodus*, (c, c') *Prioniodus*, (d, d', d'', d''') *Hindeodella*.
 All figures about $\times 27$.



teen probably represent two distinct species of the same genus.

Assemblage Sixteen

Plate 59, figure 16

Fragments of three or more *Hindeodellas* make up this group. It is similar to Assemblages Four and Six.

Assemblage Seventeen

Plate 59, figure 17

This assemblage consists of only two individuals. The left member is a beautifully preserved specimen of *Bryantodus*. It is of the clear amber type with sharply pointed, cream-colored denticles deeply set into the bar. The right member is a specimen of an undescribed type of conodont, having two parallel rows of laterally fused denticles. Only one row is visible in the picture. The specimen is dark amber in color. This combination is very common and many examples have been found.

Assemblage Eighteen

Plate 59, figure 18

An excellently preserved group of individuals is represented in this assemblage, but unfortunately, their orientation has not remained undisturbed. They have been twisted out of their original position, and for sake of clarity in description, the posterior end of the assemblage has been assumed to be occupied by the forms of *Hindeodella* and *Prioniodus*.

The most posterior forms are a pair of *Hindeodellas*. These specimens are unique among all *Hindeodellas* which have been observed by the writer. The anterior end of the upper individual is anteriorly located in the assemblage as it is now oriented. The lower member is almost entirely covered by the upper member. Its anterior end appears to be diametrically opposed to the corresponding end of the upper member. In fact, the ends of the two members are so closely fitted together that they appear

to be fused. However, this may be a matter of chance. To the right of this pair is another excellent specimen of *Hindeodella* with its denticles pointing outward and the main cusp posteriorly located. At the anterior end of this specimen is the imprint of a fourth *Hindeodella*, the denticles of which point inward. In the posterior half of the assemblage occurs a well-preserved pair of *Prioniodus*. The denticles of the left-hand member point posteriorly with the main cusp on the inside. The right-hand member of *Prioniodus* lies with its denticles pointing to the right and the main cusp on the posterior margin. In front of the pair of *Prioniodus* is a pair of *Bryantodus*. The denticles of both of these individuals point posteriorly and the two bars are close together. In the anterior part of the assemblage is a pair of conodonts unknown in our modern scheme of classification.

CONCLUSIONS

A study of the photographs and outline drawings on Plates 58 and 59 brings out a number of interesting relationships.

1. Conodonts are paired.
2. They are made up of right and left groups.
3. The pairs are laterals instead of uppers and lowers. In some cases it appears as though they may have been grouped around the mouth opening as in the mouth of a modern annelid. This is an interesting condition and is not suggestive of fish teeth. This situation would also indicate that there was not an upper and a lower jaw, a condition essential to vertebrate animals.
4. There are only a few pairs in each mouth. This appears to be a very essential and important observation because if they occurred in the mouth of a fish, we would expect to find many pairs, or at least, many teeth. But, in no case have more than ten conodonts been observed in one assemblage.
5. In many assemblages examined there are as many as four pairs of teeth

of different architectural design in one mouth. The various pairs represent as many different genera in our present scheme of classification. If these teeth belonged to such an animal as a Myxonoid we would expect to find numerous forms that were identical or at least similar in their general structure, but never the diversity of form that is found.

After extending their study of conodonts to "such recent fishes as the Myxines and small Selachians," Ulrich and Bassler (2) "feel certain the prevalent opinion that many kinds of these teeth may occur in the same mouth, or plates in the same dermal armor, is not warranted by the facts. Except that there are right and left pairs belonging in the case of teeth, to the right and left sides of the upper and lower jaw, the minute teeth, wherever located in the mouth of the supposed living relatives of the conodonts, are essentially alike and thus each kind is characteristic of some particular genus and species."

The conodont assemblages herein described definitely prove that teeth of various kinds, representing more than one genus in our present scheme of classification, existed in the mouth of one individual. Particular attention is called to Assemblage Number Eighteen where *Hindeodella*, *Prioniodus*, *Bryantodus* and one undescribed genus occur.

6. There is a tendency for the largest pairs to be posterior.

7. Six sets of identical assemblages have been found. This would indicate that the preservation was not accidental but natural. Other assemblages are similar to these six identical sets.

8. All of the isolated conodonts in this shale have been recognized as integral parts of known assemblages. This indicates that all conodonts are parts of some kind of a jaw apparatus.

9. There is a lack of a definite pulp-cavity in the denticles of conodonts. A pulp-cavity is invariably found in the teeth of vertebrate animals.

10. Even though the preservation has been perfect enough to make available

for study certain of the conodonts in their original association, no other parts of the animal have been observed. This would lead to the conclusion that the animal had no other hard parts, such as scales or bones, to be preserved, but was composed of soft tissues.

11. Some conodonts are fastened or attached in only the posterior or medial portion, whereas the other end is free. This method of articulation is a condition which seems impossible in fish, but is actually the case in annelid worms.

12. Teeth or tooth-like structures are found in the jaws of some arthrodires and acanthodian sharks. However, the architectural design of individual conodonts, the number and arrangement of parts in the "assemblages" show no resemblance to the jaw parts of these forms.

13. There have always been mechanical difficulties in fitting the varied and complicated parts of conodonts into the mouth of a vertebrate. This is not the case with worms. Similar complicated structures are found in modern annelids and are mechanically operated by muscular attachments.

14. All students of conodonts have necessarily observed the perfect preservation of the minute, delicate and sharply pointed denticles. These denticles could not have been used as masticatory apparatus; they would have been worn and the points broken off. However, they could be used in the mouth of annelids to aid the animal in obtaining food without any, or at the most very little, mechanical wear. This is the main use that modern annelids make of their teeth.

15. The arrangement of the assemblages observed in the Quadrant shale of Montana is similar to that in modern annelids.

16. The component parts may be directly compared to the individual parts of the jaw apparatus of modern annelids.

17. There is a repetition of the same specific type of conodont in various assemblages, but in no case is there a mixture of different specific types of one genus in an assemblage.

18. The associations are not due to coprolites. Coprolites are unknown in this shale. The matrix is never discolored around or within an assemblage. The writer has seen many coprolites that contained a heterogeneous group of conodonts and is well acquainted with their nature.

To summarize these points in the discussion of annelid affinities of conodonts, we find that annelid jaws are paired, various structural forms occur in one mouth, they are commonly rights and lefts, or laterals; fewer pairs of teeth are contained in the mouth of an annelid than in the mouth of a fish; individual parts seldom show any essential wear; a muscular attachment is present, and there are no other hard parts present to be preserved.

To the writer it now seems impossible for conodonts to belong to any group of animals other than Vermes. All of my observations indicate such a zoological affinity. Furthermore, there is nothing in the assemblages studied, and herein described, that is opposed to such a conclusion. The many points which have been enumerated make it practically impossible for them to be considered as fish. In spite of these seemingly dogmatic statements, it is realized that the animal which bore conodonts has not been seen; nevertheless, all observations and all evidence available to the writer, point to annelids as the natural possessors of conodonts.

It is probable that one family of Paleozoic annelids possessed a jaw apparatus composed of teeth which we call conodonts; whereas, a second family possessed teeth known as scolecodonts. Those possessing conodonts died out at the close of the Paleozoic; whereas, that family having the scolecodont type of teeth lived on to the present, giving rise to such forms as the modern *Nereis* and relatives.

CLASSIFICATION OF CONODONTS

Conodont assemblages are not well enough known at this writing to warrant a combination of genera. Furthermore, the writer realizes the impossibility of differentiating the species of an isolated conodont if genera were combined. Therefore, to facilitate the practical use of conodonts, no changes in classification are suggested or deemed advisable at the present.

The writer will make extensive searches for additional assemblages during the summer of 1935.

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